BIRD DISTRIBUTION AND ECOLOGICAL CONCEPTS

A SYMPOSIUM DIRECTED BY V. E. SHELFORD [1]

PART I

THE CONCEPT OF THE BIOME AS APPLIED TO THE DISTRIBUTION OF NORTH AMERICAN BIRDS

BY EUGENE P. ODUM

IN discussing such broad topics as the relation of bird distribution to ecological concepts, one can easily become entangled in an effort to follow the various lines of thought suggested by the observable facts. In this, the introductory paper of the symposium, I shall therefore attempt to clarify and simplify rather than elaborate, presenting first a simple comparison of the life zone and biome theories, and second, a discussion of the theoretical and practical aspects of the biome concept as applied to the distribution of birds during the breeding season in North America. Since there are a number of recently published papers to which the reader may refer for definitions, details, and further explanations, I believe that I can best present my material in semi-outline form.

Classification by Community or Environment

Ecologists are often accused of creating a hierarchy of terms or systems of classification and then trying to fit all situations to them; hence it may be well to say a few words in justification of setting up systems for ecological classification even when knowledge is still in a formative state. From the time of John Ray and Linnaeus, the need for an orderly system of naming organisms has been universally recognized. But organisms do not occur in nature in such taxonomic groupings nor do they exist independently of one another; hence it is logical, as well as important, to study and classify them by their natural groupings (i.e., by actual communities). However, distributional classification is not an end in itself any more than taxonomy is. It is merely a useful tool in research; a method of organizing the manifold detail of field observations; a specific means of stimulating and directing research; an aid in orienting the student of distribution.

A new theory always stimulates investigation, but progress seems to be even more rapid when an opposing viewpoint is also presented. Witness the tremendous impetus given to biological study by the epigenesis *vs.* preformation and the evolution *vs.* non-evolution controversies. Work on classification by communities or environment has led to two important theories of distribution: Merriam's life zone system and the

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more recent biome system.[2] Discussions of these two theories have provided and undoubtedly will continue to provide a growing incentive for the study of the ecological aspects of distribution.

The Life Zone Theory

History. "Life zone," as a term, is too well known to ornithologists to require explanation. The life zone system was developed by C. Hart Merriam between 1890 and 1895 after he had observed the sharp "zonation" of life on San Francisco Mountain, Arizona. Impressed with the importance of temperature as a determinant, he formulated two temperature laws (Merriam, 1894:236) and mapped six zones as transcontinental bands along temperature isotherms (Merriam, 1898: map). Under Merriam's dynamic guidance, the life zone concepts had an important unifying influence on the pioneer field work of the U. S. Biological Survey and on the work of ornithologists generally.

Theoretical basis. Although temperature, which Merriam used as the basis (limiting factor) of his life zones, has proved time and again to be important, his temperature laws have not proved in practice an adequate basis for setting up major divisions of plant and animal life. Obviously, the actual distribution of organisms must serve as the basis of any logical, useful division and is, in fact, the basis used in the more recent discussions and mappings. (Merriam's two temperature laws have been criticized in detail by Livingston and Shreve, 1921; Kendeigh, 1932; Shelford, 1932; and Daubenmire, 1938.)

Application to actual distribution. Most of the recent applications of life zones have been concerned with restricted areas such as a mountain range or a single state (political unit), rather than with the fauna of an entire zone or with the entire distribution of any one species. Boundaries and bird "indicators"[3] have been set up for each locality, usually without much attempt to relate the locality to the continental zone as a whole, and when applied in this way to local distribution problems, life zone terminology has proved convenient to ornithologists. However, efforts to correlate such local studies have shown that the ranges of bird species agree well with Merriam's Arctic and Canadian zone divisions, but poorly or not at all with the Hudsonian, Transition, Upper Austral and Lower Austral zones. The Transition, Upper and Lower Austral zones, particularly, are not natural biotic units because they cut from east to west across regions of widely differing vegetation and avifauna. Dice (1923:43–44) points out that the life zone theory is "founded on the belief that there are zones of life extending transversely across the continent of North America, in the south as well as in the north;" that "belts of life do occur in the northern part of North America and on mountains, yet the recognition of transcontinental zones

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[2] I have not made a detailed critical study of a third system of distributional classification (by "biotic provinces") recently proposed by Dice (1943).

[3] Specific organisms indicating the presence of certain conditions.

of life in the southern part of the United States seems contrary to the facts of distribution." This is the criticism most often made against life zones (see Ruthven, 1920; Shelford, 1932; Daubenmire, 1938; Pitelka, 1941).

Many indicators (or species characteristic of a given zone), such as those listed by Chapman (1932:32–34), fail to fit even remotely the zones they are supposed to represent. Thus such wide-ranging species of "seral"[4], or developmental, habitat as the Mourning Dove, Meadowlark, Bobwhite, or Kingbird, can hardly be considered characteristic simply of the Transition zone; nor are the Tufted Titmouse, Cardinal, Carolina Wren, and others, which Chapman (p. 33) lists for the Upper Austral, any more characteristic of that zone than of the Lower Austral.

The longitudinal division of the austral zones (i.e., the Transition, Upper Austral, and Lower Austral) into humid and arid portions helps to correct the above-mentioned failings of the life zone system but is not altogether satisfactory, since these divisions are highly arbitrary from the standpoint of environments. Obviously, the diverse conditions east-west across the continent require a number of major longitudinal divisions.

The original life zone concept more or less ignored the vegetation as a primary factor on the theory that although climate controls both fauna and vegetation, it affects one independently of the other. An increasing tendency has been evident, however, to base life zones on the vegetation; thus, "Canadian zone" in the minds of most ornithologists means "northern coniferous zone," and it is obvious that the "botanical" term describes the area far better than the "political" term. Biotic factors in general (both faunal and floral) have received more and more emphasis in the modified life zone concept of today (see Brooks, 1940:252–253, for example). Grinnell (1928; 1943:194) divided life zones into "associations," and associations into "ecological niches." Both terms emphasize community rather than temperature alone, and such shifts in emphasis direct attention to the fact that the terminology of the life zone system needs to be redefined or to be replaced by a more descriptive one.

Advantages of the concept. In bird study, the life zone theory has certain obvious advantages over other theories; most important among these are: (1) familiarity through long use by ornithologists and mammalogists; (2) simplicity and convenience (bird students find the concepts and terminology easy to grasp); (3) conformity with the evolutionary viewpoint in that it emphasizes the importance of temperature (climate) as a barrier to the northward and southward (and altitudinal) spread of species and genera.

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[4] A "sere" in biogeography is the complete cycle or "series of communities that follow one another on any given area of the earth's surface" (Carpenter, 1938:242), from initial barrenness to the final, "climax" formation (as, for example, coniferous forest).

THE BIOME THEORY

History. The concept of an association of diverse, mutually dependent organisms in a natural ecological unit (biotic formation, or biome) has had a gradual development which began at least as far back as 1877 when Mobius used the term "biocenose" for such an association or community. The studies and writings of Clements (particularly his 1916 plant succession monograph and subsequent work) and the work of Shelford have given wide currency to the concept in North America. In other parts of the world, similar concepts have been found useful by other workers, for example, C. G. J. Peterson, in his work on marine communities; J. F. V. Phillips in his work in South Africa; Palmgren in Finland; and W. N. Beklemischev in Russia. A detailed history and discussion of the biome theory in general is given by Clements and Shelford (1939); Pitelka (1941) has studied the distribution of North American birds in relation to the major biomes.

Definition. Biomes may be defined as major biotic communities, that is, natural groups of organisms characterized by the occurrence of certain plants and animals which are *dominant* (in the ecological sense of "controlling" the group and habitat) and *influent* (that is, exerting an important influence on the group and habitat). Since plants are usually *dominant* in terrestrial habitats, biomes are largely determined by the vegetation, specifically by the "climatic climax" [5] vegetation, but also by the important (i.e., *influent*) animals. Hence a biome map is not simply a vegetation map. Vegetation provides the background, as it were, but the occurrence of certain animals actually determines the major divisions; for example, although the northern coniferous forest biome is made up of several distinct plant "associations," the area is given unity by certain plants and animals ("binding species") whose range extends through all of the associations (Shelford and Olson, 1935:375–378).

COMPARISON OF LIFE ZONES AND BIOMES

In the life zones and biomes of North America (compare Chapman, 1932: end paper map, with Pitelka, 1941: Figure 1) the most obvious differences are as follows: (1) For the transcontinental austral zones of the life zone system, the biome system substitutes a number of community centers (biomes) east to west across the continent. (2) In the life zone system there is but one "transition" zone, but biomes are separated by a number of areas of overlap, or transition, called *ecotones,*[6] whose width depends on the rapidity of change, which, in turn is often determined by the topography (for example, often a biome is on high ground, the adjoining one on low).

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[5] "The community in which an area ultimately terminates" (Carpenter, 1938:58).

[6] One of the most interesting ecotones that I have visited is the aspen parkland region of western Canada, which is a "three-way" transition area. Not only do coniferous forest species and grassland species meet here, but the breeding ranges of a number of typical eastern deciduous forest species (for example, the Redstart and Rose-breasted Grosbeak) have westward extensions through this region (Lincoln, 1935:37).

But it is in their approach to distribution problems that the fundamental difference lies between the life zone theory, which emphasizes the effects of physical factors on species or other taxonomic groups, and the biome theory, which emphasizes the development and distribution of communities. In many areas (especially in mountainous regions), the boundaries of life zone and biome units coincide; and there life zone maps differ from biome maps only in the names of the areas, employing the geographical (political) terminology of that theory instead of the biotically descriptive names of the biome theory.

Bird Distribution and the Biome Concept

The biome theory does not minimize the effect of temperature as a limiting factor but it takes into account other features of climate and recognizes the direct importance of cover (shelter or habitat). The organisms themselves are used as indicators, on the assumption that they are collectively better "judges" of the conditions than any measuring device yet invented by man. In the final analysis, the arrangement of biomes and their sub-units gives about equal emphasis to climate and cover. They are not the only limiting factors, of course, but on a continent, they are assumed to be the most important for the majority of species. Let us examine these and other factors in order to see if this is a logical assumption, particularly in relation to birds.

Climate. The climate of any given area is of such undoubted importance in determining all the life forms that little need be said except to point out that such factors as rainfall, humidity, wind, and solar radiation, are important as well as temperature. The climax vegetation is probably the best indicator of the sum total of climate (Clements, 1920:63–64). A map of climaxes is a much better map of climates than is a map of any single climatic factor.

Cover (*shelter or habitat*). Not only is habitat all important in determining local distribution, but it is increasingly recognized as a major factor in limiting the overall range as well. Its importance is clearly shown by the spread of certain species into areas (formerly unoccupied by these species) after changes in vegetation (cover) have occurred there even without change in climate. One could list numerous recent examples of this, such as the spread of the Robin into the grasslands after the planting there of trees, the southward spread of the same species with "opening up" of forest and planting of lawns, the spread of Prairie Chickens into the coniferous forest area of Wisconsin after deforestation, or the eastward spread of the Prairie Horned Lark into extensive man-made grasslands in the eastern deciduous forest area. On the other hand, many other species fail to spread even when suitable habitat is available or made available; for example, the Wood Thrush, Eastern Wood Pewee, or Crested Flycatcher have not (as yet) spread into extensions of the original deciduous forest; in these cases climate (or some factor other than cover) may be the major limiting factor. Thus, the activities of man that produce changes in cover without change in climate may enable us to determine which of the two factors is the more limiting for particular species. Otherwise because of our present lack of knowledge of basic physiological and psychological responses of birds, it is by no means easy to come to a conclusion on this point. For example, J. J. Murray (1940:57), who has given us some excellent observations on the zonal distribution of Virginia mountain birds, observes that the Yellow Warbler occurs commonly in the valleys but not in clearings or orchards at high altitudes. Murray concludes from this observation that habitat is not limiting in this instance, whereas I would draw the opposite conclusion for the following reasons: Since the Yellow Warbler breeds far to the north (to the limit of willows on the tundra's edge) there would be no reason to suspect that climatic conditions on even the highest mountains in Virginia would be too rigorous for this hardy species. Topography and habitat, on the other hand, would be definitely against the species since suitable breeding habitat at high altitudes in Virginia is very limited in area and isolated by extensive stretches of unsuitable habitat. If the clearings at high altitudes became more extensive and sufficiently connected with lower areas I would be willing to predict that the Yellow Warbler would eventually invade them. The extent and position of apparently suitable habitat must be taken into consideration. In the other examples (tanagers, Veery) listed by Murray in the same paragraph, the evidence for climatic limitation is much clearer, but even in these, community factors cannot be ruled out completely.

Physiographic barriers. Though a primary consideration in limiting an island group, physiographic barriers in a large continuous land mass such as North America are obviously of less importance (as compared with habitat and climatic barriers) so far as distribution of birds is concerned. Physical barriers are, of course, indirect determinants of biomes since they greatly affect climate and vegetation.

Food. Although very important in determining the local distribution and abundance of birds, food rarely seems to determine the actual range of a species. The periodic fluctuations in populations of small mammals, for example, definitely affects the abundance and breeding of tundra hawks and owls, but since such mammal food is available in virtually all regions, its occurrence on the tundra is probably not a factor in restricting the range of tundra bird species. In other words, it is the exception rather than the rule to find correlation of the range of a bird species with the range of a specific kind of prey as, for example, the ranges of the Everglade Kite and Limpkin (J. B. May, 1935:18; Harper, 1936) seem to be correlated with the distribution of the snail *Pomacea* (*"Ampullaria"*).

Biotic interactions (*coactions*). The role which competition and predation play in limiting ranges is not yet well understood. It is of undoubted local importance just as food is, and may be a factor in limiting the spread of some species. We need to know more about the alleged limiting relations between such pairs of species as the Whip-poor-will and Chuck-will's-widow, the Bewick's Wren and House Wren (see, for example, E. V. Miller, 1941:84).

"Life form" of plant vs. *species of plant.* In general, few species of birds are restricted to a particular species of plant, but many birds seem to be limited to a particular type ("life form") of vegetation. For example, many species have a distinct preference for coniferous forest, but it may not make much difference whether it be spruce, fir, or hemlock. Thicket birds select bushy growths of a specific density rather than of a particular shrub species. Grassland birds may be equally at home in beard grass, mesquite grass, or bluegrass, if the stands are of the same general density or appearance. As Grinnell (1943:183) once remarked, "the presence of a certain kind of perch or particular sort of forage surface is practically essential to the presence of a given kind of bird whose structures and instincts are adapted to it." More adequate means of measuring the importance of this "structural" feature of the vegetation are greatly needed. Many species are very adaptable to changing *species* of vegetation (for example, when cultivated grasses replace native prairie grasses—Bennett and Hendrickson, 1939), but are unable to adapt to a new *life form* or even to small changes in habitat *structure.* Within a biome, it is the *life form* of the climax vegetation that tends to be uniform rather than the *species* of the dominant plants.

Conclusion. Considerable study may be necessary to determine the critical limiting factors for individual species. For "stenothermic" species (species with limited climatic tolerance), climate will prove to be limiting at least somewhere around the range boundary; for species with wide climatic tolerance (like the Robin), habitat or other factors may be limiting. In general, however, climate and habitat seem the most important. Therefore, a classification system (such as the biome theory) that considers both these major factors, as well as intra-community relations in general, is bound to produce a better correlation of its divisional units with the distribution of a larger number of species than a system based on one factor alone.

Evaluation of Biomes

Climax and seral communities. It is important to distinguish between *climax* and *seral* (developmental) communities since bird distribution is greatly influenced by the dynamic nature of succession.

"The last community of . . . a succession is the *climax* which is self-perpetuating and is characterized by a life-form of the dominants, such as grass, deciduous forest, etc. The dominants of developmental stages within a climax region may or may not be of the same life form, as, for example, seral stages in the deciduous forest climax may include herbs, grasses, shrubs, and both coniferous and deciduous trees" (Pitelka, 1941:115; see also Weaver and Clements, 1938: chap. 3).

Thus the habitat of early seral stages is often very different from that of the climax, with corresponding differences in avifauna. These differences *within* a biome should not be confused with differences *between* biomes.

When the climaxes of different biomes are compared, each is seen to have a very characteristic group of birds. Comparatively few species occur in the climax of more than one biome—which helps give the biome its identity as a natural community. Not all climax species, of course, have ranges that exactly correspond with the biome. When a species does not occupy all its biome, or when it spreads to other biomes, the ecologist's attention is focussed on the special factors limiting that particular species, just as a "difficult" genus stimulates the work of the taxonomist.

It is not uncommon for a species to occupy the climax of one biome and the seral (developmental) stages of one or more others. The Red-eyed Vireo, for example, occurs abundantly in three biomes, but occupies the climax only in the eastern deciduous forest biome, being restricted in the coniferous forest biome to developmental communities (e.g., aspen) and in the grassland biome, to "colonies" of sub-climax forest (e.g., streamside forests).

The most widely distributed species such as the Song Sparrow, Yellow Warbler, Mourning Dove, Red-wing, and various water birds, breed in the early developmental stages of vegetation. The early developmental stages (unlike the climaxes) of widely different regions often have a similar appearance and thus offer suitable habitat for species with wide climatic tolerance. A marsh, for example, provides much the same sort of habitat in various biomes. We would expect, therefore, that "seral" birds would show less correlation with biomes than "climax" birds do; but while this is generally true, many early seral birds are restricted to certain biomes or sub-regions, the climatic (or "non-habitat") features of the community apparently holding them there.

Primitive vs. *disturbed conditions.* It is important to distinguish between primitive, or natural, conditions (by which ecological units are delimited) and disturbed conditions directly or indirectly produced by man.

Man has perhaps changed the climate little, but he has greatly modified shelter, food supply, and other "habitat" factors. Man tends to produce a forest edge condition wherever he settles, whether in forest or grassland, that is, he thins the forest, creating openings, or, in grassland, plants trees. In general, he increases greatly the areas occupied by seral vegetation at the expense of the climax areas. The sharp natural differences between regions are thus reduced, and "forest edge" species with wide climatic tolerance are encouraged to spread. Thus, lists of *roadside* and *farmland* birds which we compiled on a 6,000-mile trip through western North America were monotonously the same regardless of the biome (or life zone) traversed, whereas birds of *natural* communities were excitingly different from biome to biome.

Man's indirect influence is, of course, felt far from his habitations. Lumbering (plus forest fire) and overgrazing have produced extensive fundamental changes both in vegetation and bird populations. In the central Alleghenies the effect of such changes on breeding warblers has been carefully analyzed by Brooks (1940); in Manitoba one sees aspen forests and Red-eyed Vireos over a wide area where (to judge from the prevalence of charred spruce stumps) spruce and warblers once were; in some places, destruction of the climax vegetation is so complete that the forest may, for lack of seed trees, never be restored; likewise, huge areas of western Texas, New Mexico, and Colorado that once were grassland are now sage brush or mesquite desert. Such alterations produced and maintained by man and domesticated animals are often called "disclimaxes" and should not be confused with the true or potential climax, which is determined by climate.

Man, of course, *directly* modifies the distribution of a few birds through the introduction of exotic forms, "control" by direct predation (hunting, destruction of "undesirable" species, etc.), and through wildlife management.

Biomes are based on the primitive or potential conditions. This is not only convenient, but provides the point of reference for evaluating man's influence on his environment. Thus, preservation of primitive areas is desirable not only from the esthetic point of view but from the practical one as well, and ecologists and ornithologists should make every effort to study such natural areas in order to determine how far man has already changed conditions and how far he may change them without disastrous results.

Lack of quantitative data. In studying the correlation between distribution of species and natural areas, the lack of quantitative data is a great handicap (Pitelka, 1941:116–117). The usual check-list notations and most maps so far published are not very helpful since they indicate only the extremes of a given bird's range and fail to show where the species is really a common and influent member of a community. It would help greatly if, in describing abundance and habitat, compilers of local lists would give at least as much attention to common species as they currently give to rare ones.

Distribution of subspecies. So far in the discussion, we have considered only the distribution of full species (including, in the case of multiform, or polytypic, species, all of the subspecies). Little can be said regarding the occurrence of subspecies in relation to biomes, not only because they have not been studied from this angle, but also because the criteria used to delimit subspecies are variable, and lines drawn between races must in many cases be more or less arbitrary. As monographic studies, such as that of A. H. Miller (1938) on the Junco, have abundantly shown, morphological characters of subspecies do not "change simultaneously geographically" in transition from one extreme form of a series to the other; color, body size, length of bill, and other characters may all vary geographically although independently of one another. Nevertheless, geographical variations in bird forms are undoubtedly correlated with environmental complexes, and taxonomists should give more consideration to natural community units when dividing a species into races. Aldrich and Friedmann (1943) have recently made an admirable attempt to correlate subspecies of the Ruffed Grouse with biotic communities. Paralleling and supporting this particular emphasis (as well as the general emphasis that the biome theory gives to biotic factors) is the change in the basic concept of species, which is becoming broadly biological rather than strictly morphological (see Mayr, 1943: chap. 5 and 6).

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF GEORGIA, ATHENS